Vocal communication in the Grey-headed Flying-fox *Pteropus poliocephalus* (Chiroptera: Pteropodidae)

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ABSTRACT

The vocalisations emitted by adult and juvenile Grey-headed Flying-foxes *Pteropus poliocephalus* (Chiroptera: Pteropodidae) within daytime camps and night nurseries were studied using audio and video data. The calls were differentiated via discriminant analysis and the motor action associated with each call type was categorised. Five distinct call types were emitted by adult *P. poliocephalus* within daytime camps; *ark* calls, *harsh chuckles*, *tonal* calls, *tonal chuckles* and *chups*. The following classification was then applied to distinguish between these calls types; (1) the *harsh chuckles* and *ark* calls as 'harsh'; (2) the *tonal* calls as 'tonal'; and (3) the *tonal chuckles* and *chups* as 'intermediate' between the previous two.

Ark calls and *harsh chuckles* occurred predominantly in association with agonistic behaviours such as fighting and retaliating after being investigated by another individual; *tonal* calls were emitted most frequently when an individual was crawling or flying away from an agonistic encounter; and *tonal chuckles* and *chups* were emitted by females when a male instigated a reproductive attempt.

The physical structure of the isolation call of juvenile *P. poliocephalus* differed among individuals in terms of call length, fundamental frequency and bandwidth of the fundamental component of the call. These differences may reflect a form of 'vocal signature' that assists the mother in recognising and locating her young. It is suggested that vocal signals emitted by adult *P. poliocephalus* predominantly provide information about the arousal state of the emitter and occur in association with specific motor actions that enhance the meaning of the vocal signal.

Key words: Animal behaviour, discriminant analysis, juvenile calls, *pteropus poliocephalus*, vocal communication

INTRODUCTION

Many vertebrates use sound energy in the form of vocal signals to communicate information to other animals about themselves or about some parts of their environment (Busnel 1963; Marler 1967; Thorpe 1967; Nottebohm 1972; Lewis and Gower 1980). Squirrel Monkeys *Saimiri sciureus* emit isolation peeps when out of sight of other troop members (Schott 1975; Symmes *et al.* 1979); Gorillas *Gorilla gorilla* emit 'double-grunts' to advertise their dominance rank in the troop (Harcourt and Stewart 1996); and Western Harvest Mice *Reithrodontomys megalotis* emit squeals when defeated during a fighting episode (Fisler 1970). It has also been suggested that the 'chirps' emitted by juvenile Ringtail possums *Pseudochirus peregrinus* are a form of isolation vocalisation (Linahan 1995).

In some vertebrates, the physical structure of a call particularly whether it is of high or low frequency can often provide information about the morphology of the emitter (Ploog and Melnechuk 1967). This may be important for courtship behaviour and territory defense because if the vocal signals of an individual are indicative of their body size, the receiver may be able to assess the likelihood of winning a particular contest and subsequently avoid those where it may be defeated (Zwiefel 1968).

Within the Chiroptera, microchiropterans produce sounds of higher frequency than the Megachiroptera. The vocal cords of microchiropterans are smaller and stiffer than those of megachiropterans, structural characteristics that result in a preponderance of high frequency sounds (Suthers 1988; Pollack and Casseday 1989; Altringham 1996). Microchiropterans use sound energy in echolocation while the Megachiroptera predominantly use it to communicate acoustically with conspecifics and members of other species (Brown 1994; Grinnel 1995).

Morton (1977; 1982) recognised that in general, harsh calls that are low in frequency, noisy, and of a wide bandwidth occur most frequently in aggressive or agonistic contexts. Alternatively, tonal calls which are high in frequency and possess a narrow fundamental call component occur most frequently in fear or appeasement situations. These patterns form the Motivational-Structural Rules Hypothesis (MS hypothesis; Morton 1977; 1982; Scherer 1985; August and Anderson 1987).

Juvenile isolation calls can display a variety of 'vocal signatures' that are related to specific call structures such as length and the degree of frequency modulation, and these can form the basis on which some mothers recognise their young. This phenomenon occurs in a number of species including; the Lesser Bulldog Bat *Noctilio albiventris* (Brown et al. 1983); the Squirrel Monkey *Saimiri sciureus* (Symmes et al. 1979; Biben et al. 1989); the Vespertilionid Bat *Plecotus auritis* (de Fanis and Jones 1995); and it has been suggested to occur in the Grey-headed Flying-fox *Pteropus poliocephalus* (Nelson 1964).

The Grey-headed Flying-fox *P. poliocephalus* emits a number of different calls during roosting, feeding and flight. Nelson (1964) has described many of the vocalisations of this species and of other species of the genus Pteropus. He related these calls to a variety of activities including agonistic interactions, territorial defense and courtship.

From one month of age, juvenile *P. poliocephalus* are left in the colony overnight while their mothers fly out to feed (Nelson 1964). On their return, the mothers emit a searching call which is answered by a juvenile isolation call. This call exchange continues until the mother locates and lands next to her young (Nelson 1964). It has not been determined which aspects of the isolation call may be aiding the mother to recognise her own young.

The aims of this study were to investigate the following questions;

(1) Are distinct types of calls being made by adult *P. poliocephalus* within daytime camps?

(2) Are any vocalisation types specifically related to certain behaviours?

(3) Do juvenile isolation calls of *P. poliocephalus* possess structural differences among individuals?

METHODS

Study sites

Data were collected from two different colonies of *P. poliocephalus* at the Royal Botanic Gardens, Melbourne (37° 49' S; 144° 58' E), and Cabramatta, New South Wales (33° 55' S; 151° E). The method of data collection was the same for both sites.

Sound collection and analysis

Pteropus poliocephalus calls were collected on a Kudelski Nagra III reel-to-reel tape recorder used with a Sennheiser studio direction microphone (MKH 815T). Adult calls were recorded from both colonies during the day and juvenile isolation calls were recorded in the night-time nursery at Cabramatta. Sites were chosen at random within both colonies (see Andrieu 1963 & Wickstrom 1982 for discussion on recording animal sounds in the field).

The calls were digitised with a MacRecorder (Farallon Computing Inc.) analogue to digital converter and saved as *Soundedit* files on a Macintosh IIx computer. Audiographs were then made of the calls using *Audiograph* (1989-1990, Ralph Slater Sutherland), a sound analysis package for the Macintosh.

Based on preliminary investigation, the following variables were measured and subsequently used in a discriminant analysis;

(a) The length of each call (ms), which consisted of the single note of the tonal call types (*tonal* calls), and the repeatable unit of the harsh (*ark* calls and *harsh chuckles*) and intermediate (*tonal chuckles* and *chups*) call types.

(b) The mean fundamental frequency, which is the midpoint of the bandwidth of the fundamental component of the call (kHz). This measurement in *P. poliocephalus* will be referred to as the 'fundamental frequency'.

(c) The bandwidth of the fundamental, which is the range of frequencies across which the fundamental component of the call occurs (kHz).

The juvenile isolation call of *P. poliocephalus* is frequency modulated and appears as a series of 'arches' on the audiograph. The number of 'arches' present in the isolation call varies both within and among individuals. In order to standardise call length so that a comparison of isolation calls among individuals could be made, the overall call length was divided by the number of 'arches' and this measurement was used in the statistical analysis.

Video collection and analysis

All of the video data were collected on a Canon Hi-8mm videocamcorder (UC9Hi-8 attached to a tripod). Filming sites were haphazardly chosen from areas that were back-lit by the sun and had a moderate (50) to large (200) number of individuals present. The camera was focused on a group of *P. poliocephalus* and their activity observed and recorded through the viewfinder while listening for any associated calls. Upon hearing a locatable call within the group under observation, the camera would be zoomed in on the individual/s responsible and they were then followed with the camera until the activity ceased.

The video tape was studied for any bouts of activity that were suitable for analysis. A bout was deemed suitable if an identifiable call occurred and if the motor actions of all participants were clearly visible. For each bout, the behaviour of each participant was then analysed in detail.

Statistical Analyses

Discriminant analysis was used to determine if there was a relationship between any of the eight call types and the predictor variables of call length, bandwidth of the fundamental call component and the mean fundamental frequency. The audio data collected from both sites were pooled for the discriminant analysis.

A chi-square analysis was used to investigate the relationship between call type and motor action in *P. poliocephalus*. Again the video data collected from both sites were pooled for the chi-square analysis. A repeated measures analysis of variance (ANOVA) was used to compare differences in the juvenile isolation call among individuals.

RESULTS

Five call types were differentiated by the discriminant analysis (Pillai's trace = 1.903, f = 126.6, df = 12,876, p<03001, with 98% of the calls classified correctly, sample size = 300 individual calls), these were; *ark* calls, *tonal* calls, *tonal chuckles, chups* and *harsh chuckles* (Figures 1A-E). Figure 2 is a plot of the first two canonical variable scores for this analysis and it demonstrates

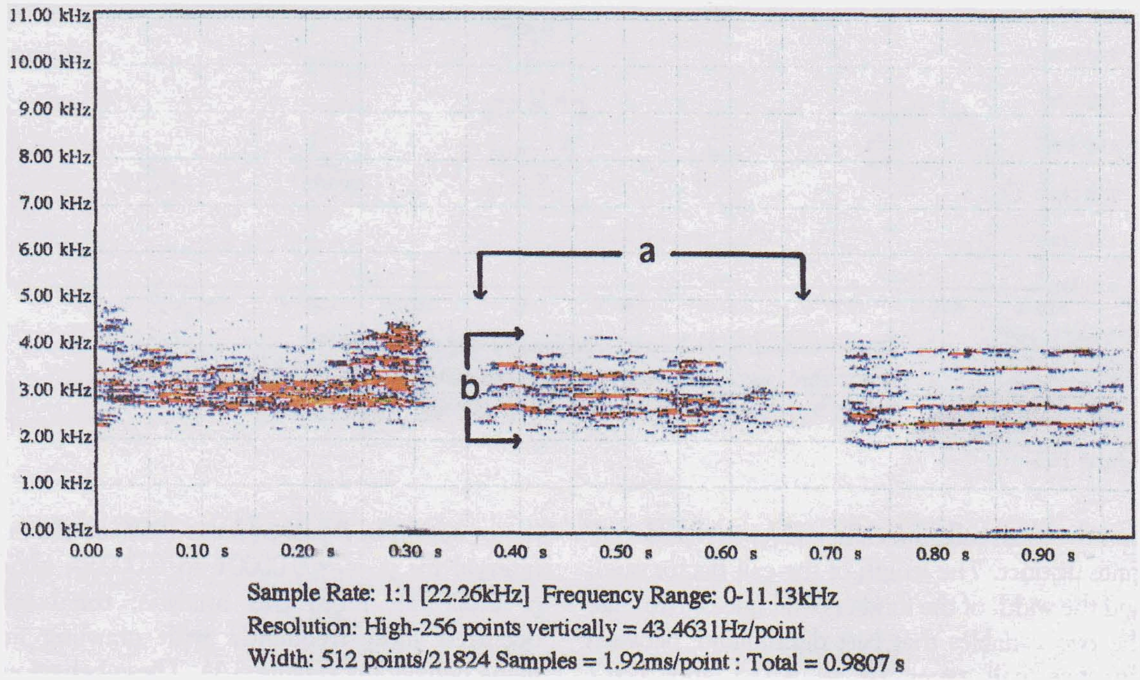


Figure 1A-E. Audiographs of the five call types emitted by adult Pteropus poliocephalus in daytime camps; A - ark calls, B - tonal calls, C - tonal chuckles, D – chups and E – harsh chuckles. The different colours represent the different intensities present within the call. Blues, reds and yellows denote the least intense parts (approximately –42 - -24 db), whilst green represents the most intense parts of the call (approximately –18 – 0 db). The y-axis delineates the range of frequencies the call is measured across (0-11 kHz) and the x-axis shows call length (0-1 second). 'a' denotes call length, 'b' the width of the fundamental call component and 'c' the width of the fundamental call component.

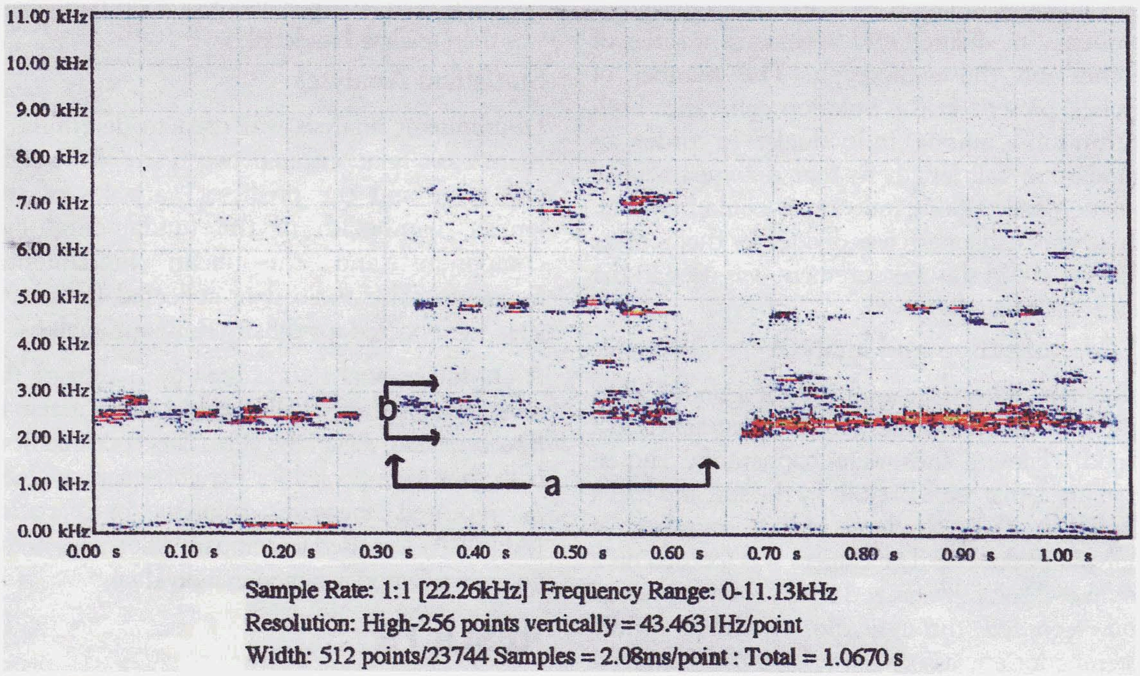


Figure 1B.

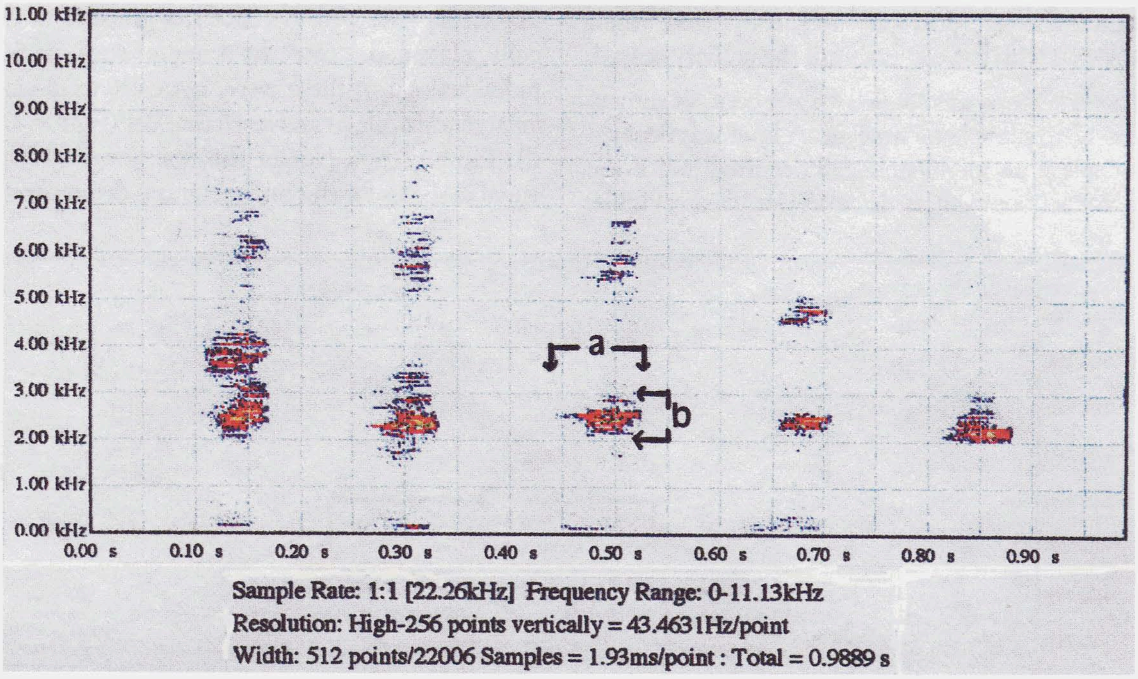


Figure 1C.

that the tonal calls, *ark* calls, and *harsh chuckles* are quite distinct. The length of the call (factor one), and the width of the fundamental (factor two), are the two variables that best discriminate between the five call types (F = 420.5 and 126.7 respectively). The fundamental frequency is the least effective at discriminating between the five call types (F = 12.18).

A Monte Carlo Randomisation test confirmed that there was a statistically significant relationship between call type and the associated motor action in *P. poliocephalus* (95% confidence interval for p = <0.00001 to 0.00030; actual p<0.00001). From this analysis, tonal calls occurred most frequently with crawling and flying behaviours (Figure 3A). These behaviours were characterised by an individual either crawling away from an aggressor along a branch or trunk (using a quadrupedal gait with the wings closed and the thumb-claws extended), or flying away from an aggressor by flapping the wings until the individual was horizontal and then

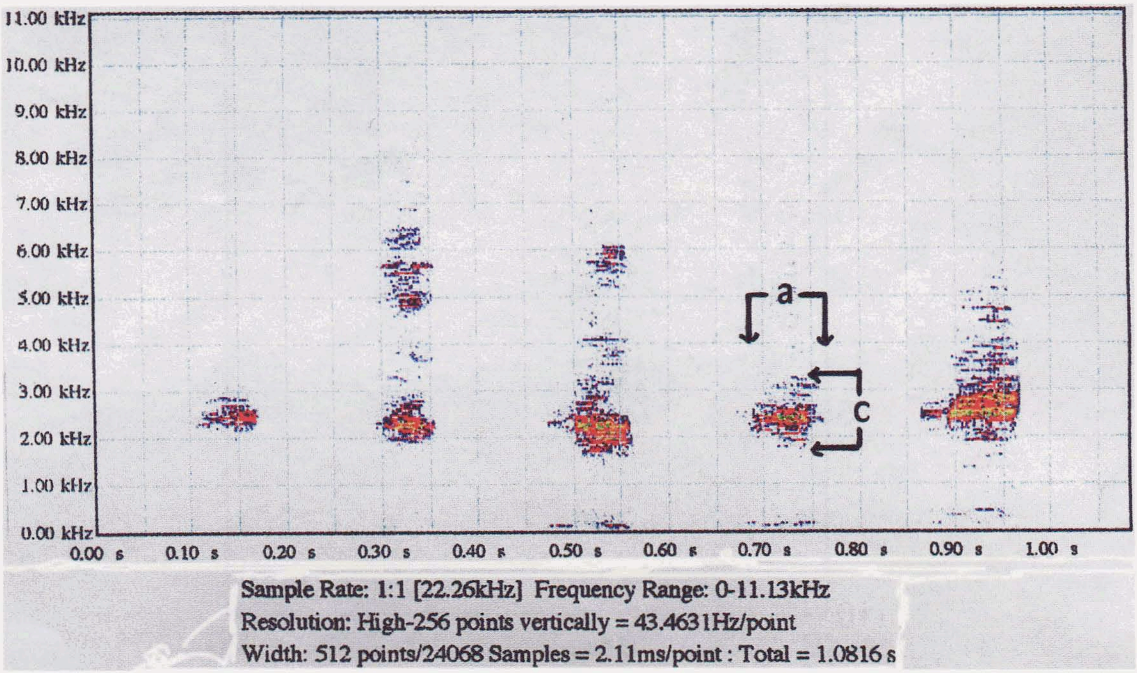


Figure 1D.

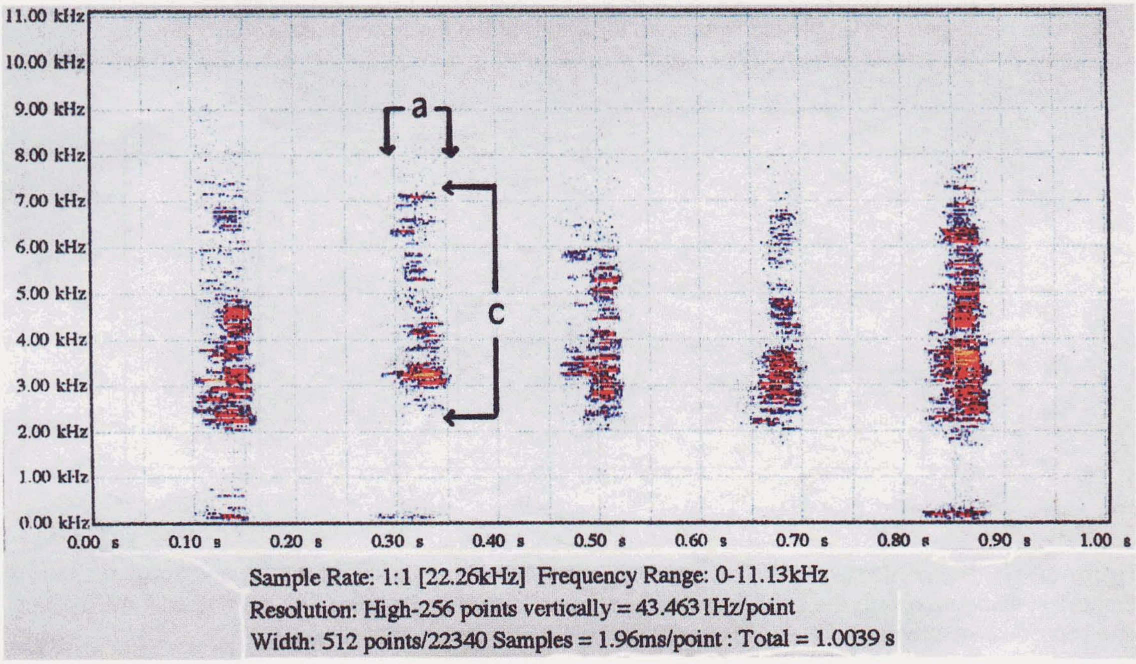


Figure 1E.

flying away from the branch (Plate 1A). Eighty-seven percent of the *tonal* calls that were made during crawling or flying behaviours were made by the individual moving away (n=15, number of replicate calls taped from different individuals).

Harsh calls were found to occur most frequently with fighting and investigative behaviours (Figure 3B; Plate 1B). Fighting behaviours were characterised by individuals flapping their wings toward each other or lunging in and attempting to bite each other. Fifty-four percent of the harsh vocalisations made during fighting were emitted by the inferior competitor, 35% were emitted by the aggressor, and 11% could not be determined (n=110, number of replicate calls taped from different individuals).

Tonal chuckles and *chups* (intermediate calls), occurred most predominantly with reproductive behaviours (Figure 3C). The male would instigate the reproductive behaviour and the female would vocalise as she was being held by and was grappling with the male (60% of calls

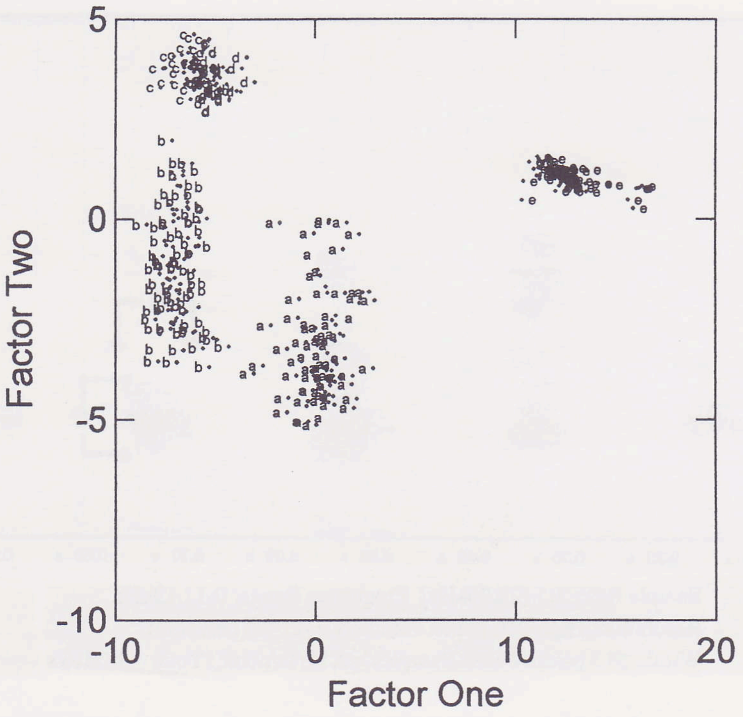


Figure 2. A scatterplot of the canonical variable scores assigned to each 'case' during the discriminant analysis. Factor one represents call length and factor two the width of the fundamental call component. Key to call types: a. ark calls (n=76); b. tonal calls (n=79); c. tonal chuckle (n=40); d. chup (n=72); e. harsh chuckle (n=29).

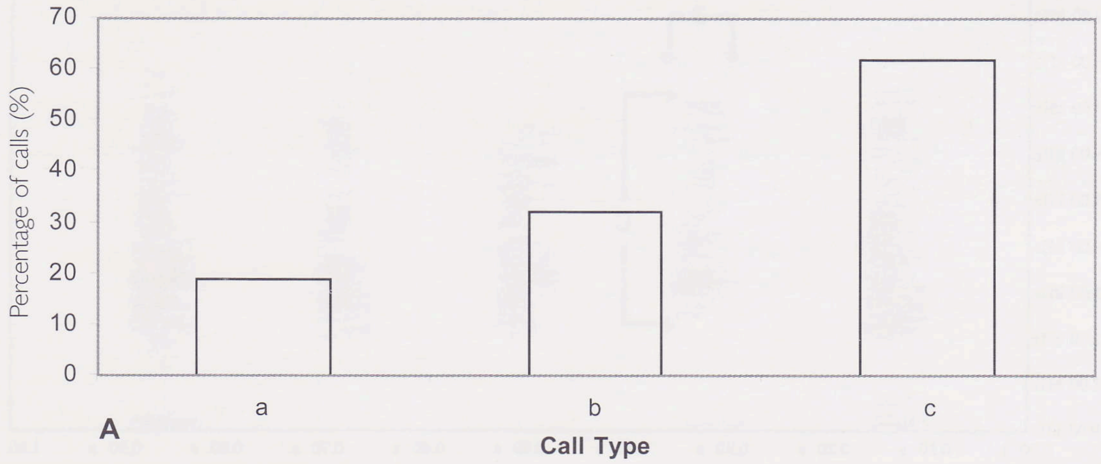


Figure 3A-C. The percentage of calls of each call type; 'harsh' (a), 'intermediate' (b) and 'tonal' (c), that were emitted in association with the behavioural categories of 'crawling' and 'flying' (A), 'fighting' and 'investigating' (B) and 'reproductive attempts' (C).

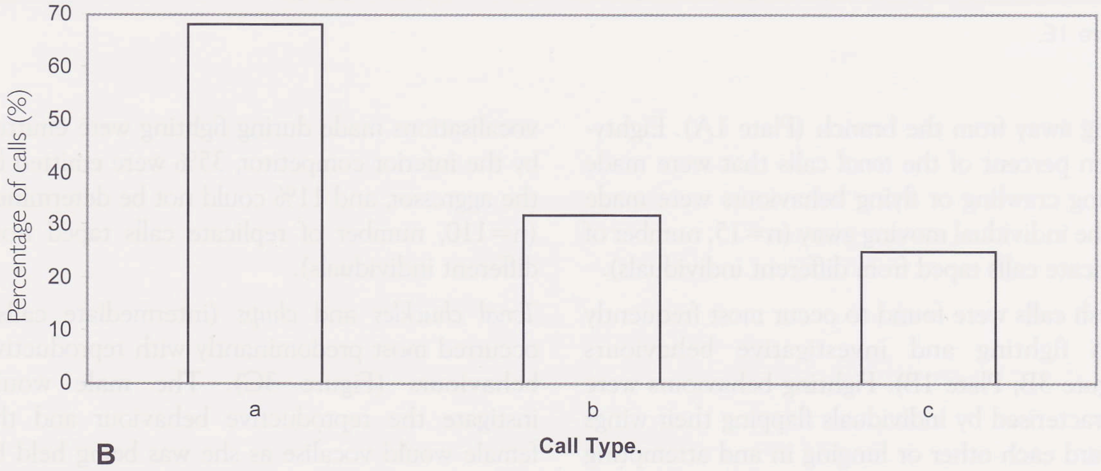


Figure 3B.

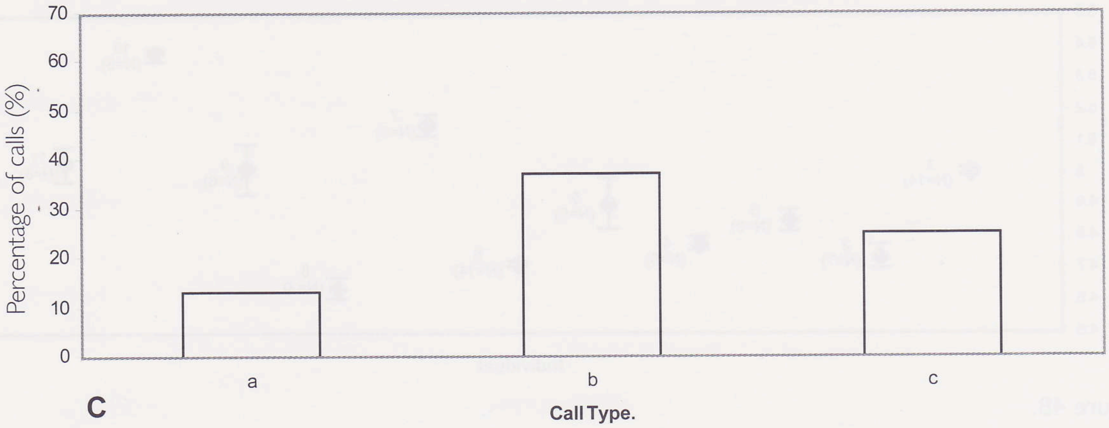


Figure 3C.

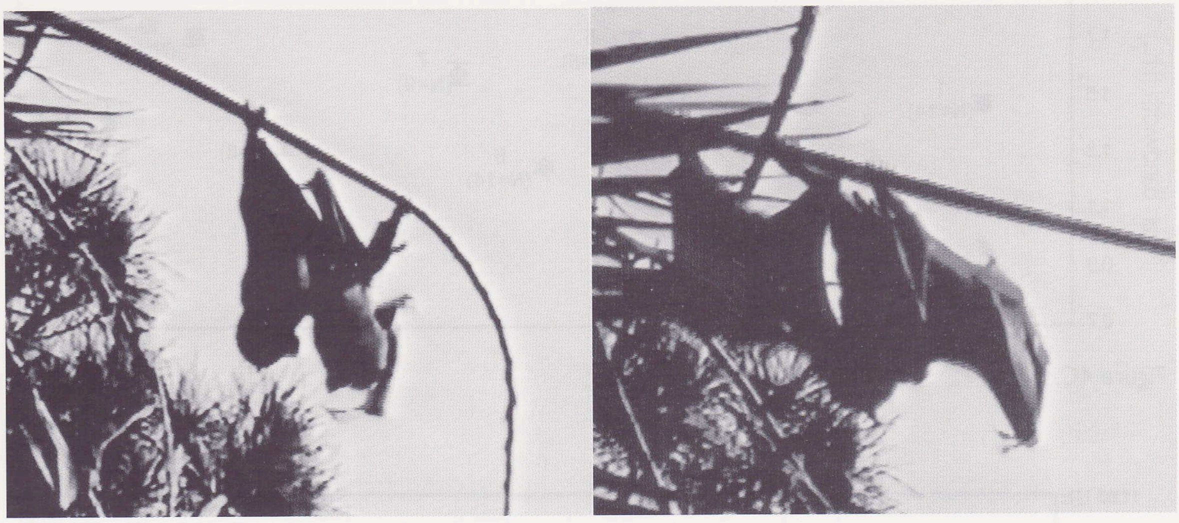


Plate 1A.

Plate 1B.

Plate 1A-B.

A. 'Crawling' behaviour in Pteropus poliocephalus. The individual on the left is crawling away after an agonistic encounter with the individual on the right. The individual on the right has followed the individual that is crawling away.

B. 'Fighting' behaviour in Pteropus poliocephalus. The two individuals here are in close but not physical contact and are directing their thumb-claws towards each other.

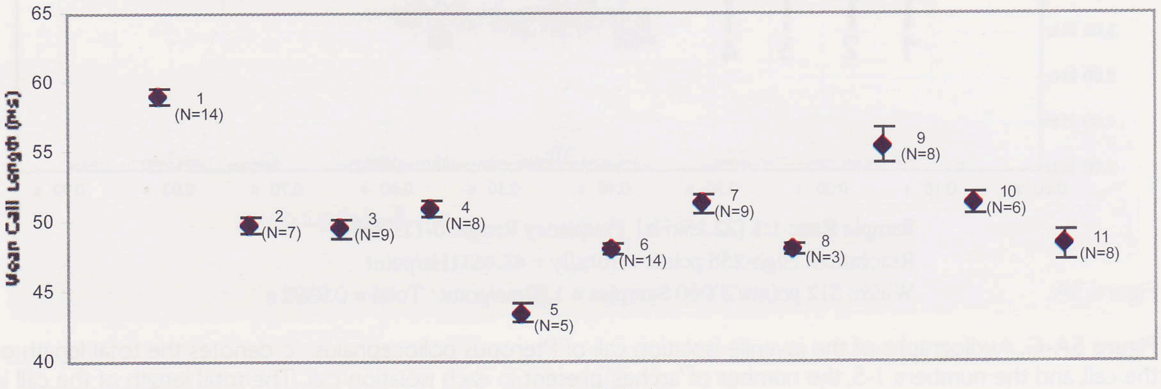
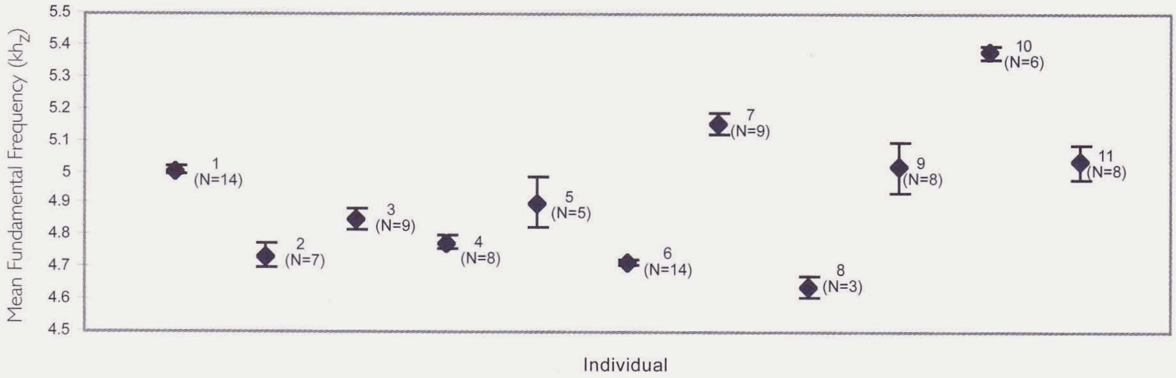


Figure 4A.

Figure 4A-C. A comparison of call length (A), fundamental frequency (B) and mean bandwidth (C) of the fundamental call component for the isolation calls of juvenile *Pteropus poliocephalus*. The numbers 1-11 represent the isolation call of a single individual.



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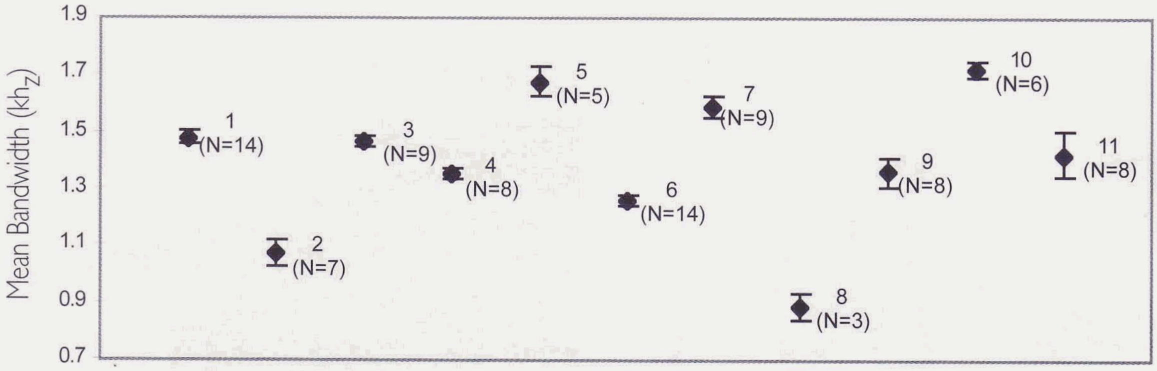

Figure 4C.

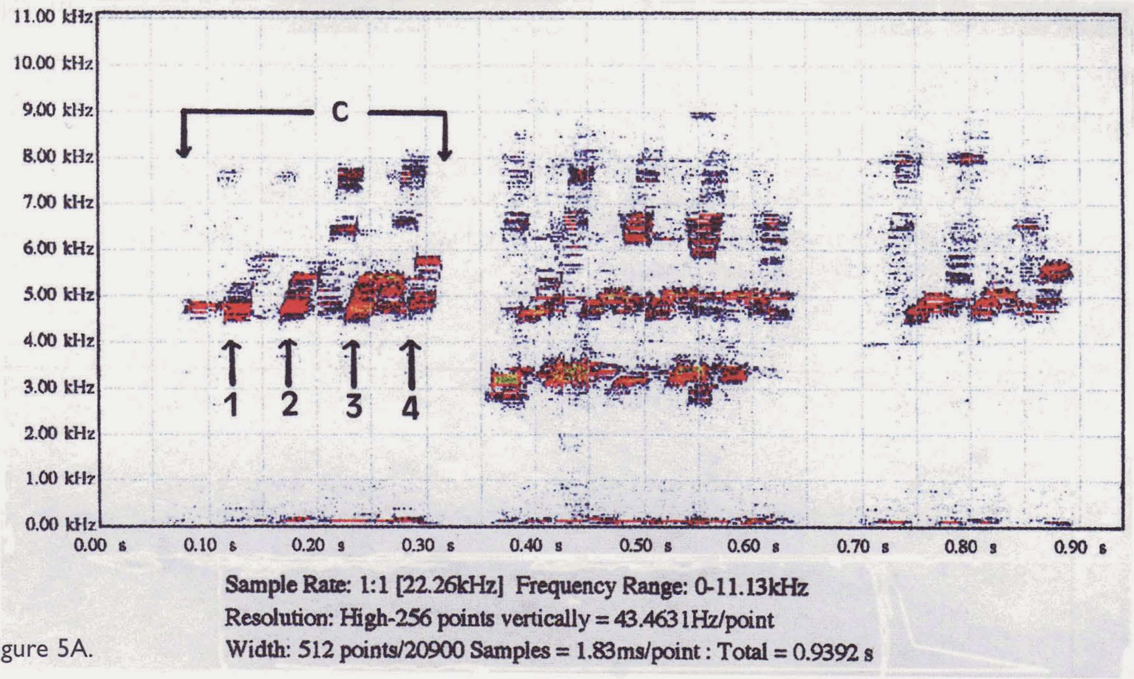

Figure 5A.

Figure 5A-C. Audiographs of the juvenile isolation call of Pteropus poliocephalus. 'c' denotes the total length of the call, and the numbers 1-5, the number of 'arches' present in each isolation call. The total length of the call is divided by the number of 'arches' to provide a value that is comparable among individuals. 'A', 'B' and 'C' are representative isolation calls of three different individuals. Note that a small gap occurs between each of the 'arches' within a single isolation call. This 'abrupt' start and end point aids in the receiver location of the call. Refer to Figure 1 for the explanation of the different colours within the call. The y-axis delineates the range of frequencies the call is measured across (0-11 kHz) and the x-axis shows call length (0-1 second).

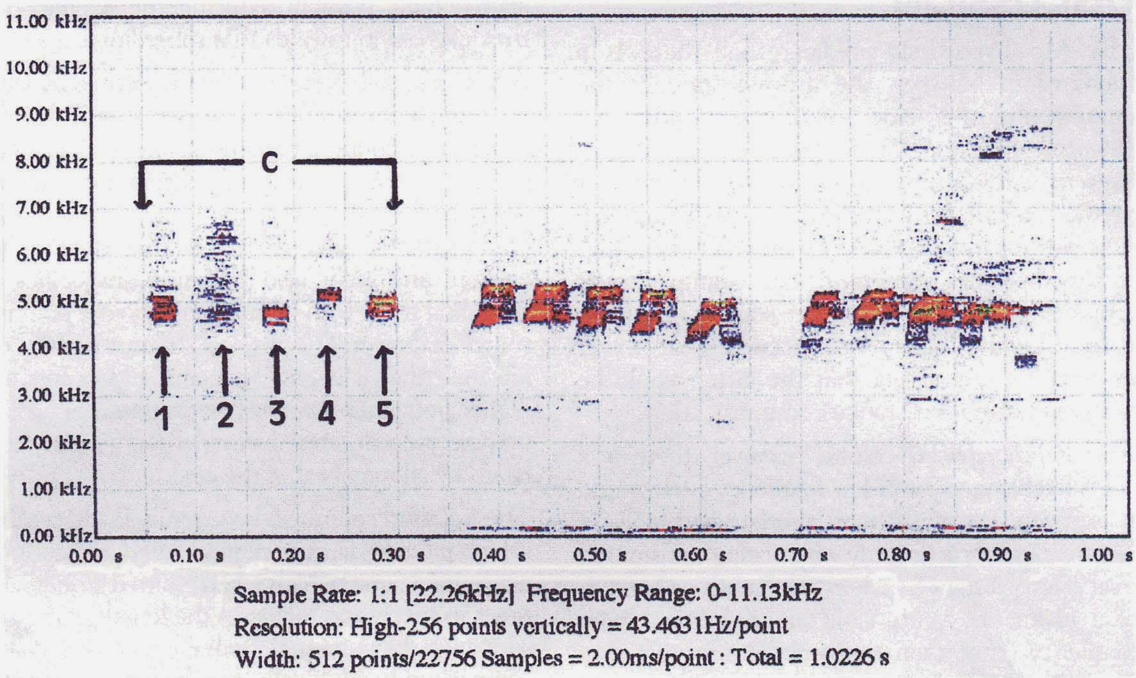

Figure 5B.

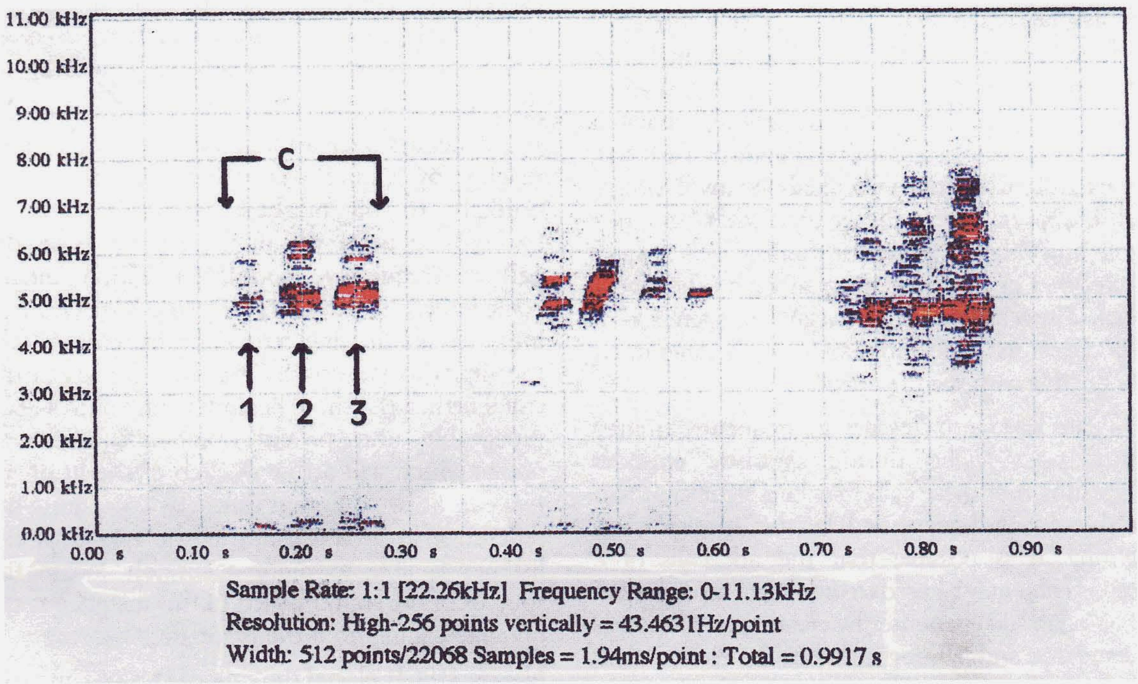

Figure 5C.

made, n=7, number of replicate calls taped from different individuals). The female was also heard to emit an intermediate call after she had stopped a reproductive encounter by moving away from the male (n=2, number of replicate calls taped from different individuals).

The isolation calls of juvenile *P. poliocephalus* were found to be statistically significantly different from each other (repeated measures ANOVA, F=11.554, p<0.001, 87 cases processed; Figures 4A-C). Three variables were tested for their importance in discriminating between the isolation calls of 11 different juveniles; (1) the length of the repeatable unit of the call, (2) the fundamental frequency of the call, and (3) the width of the fundamental of the call.

DISCUSSION

The MS hypothesis predicts that there is a relationship between the arousal state of the emitter and the structure of a particular call (Morton 1977; 1982). Morton recognised that the MS hypothesis was most effective at predicting call type in close-contact situations, however for long distance communication other factors become important. For example, over long distances, high frequency sounds attenuate more quickly than those occurring at lower frequencies, suggesting that the latter would be more effective for distance communication.

In a *P. poliocephalus* colony, however, there is a considerable amount of low frequency background noise occurring which may interfere with calls of low frequency, particularly when being transmitted over a long distance such as the length or breadth of a Flying-fox camp. Calls emitted in a higher frequency range than the background noise may subsequently transmit better over long distances in situations where this occurs.

Ark calls and *harsh chuckles* are emitted by *P. poliocephalus* when the primary receiver of the call is in close proximity. These calls are highly correlated with agonistic behaviours such as fighting, including the aggressive response after being investigated by another individual. Much of the fighting behaviour of *P. poliocephalus* is stereotyped (Puddicombe 1981), for example when two individuals are involved in a fighting episode they will face each other, bare their teeth and either extend their thumb-claws towards each other or flap their wings at each other (pers. obs.). Physical contact between the aggressors is infrequent, with the wings and thumb-claws rarely connecting with the opponent.

Ark calls and *harsh chuckles* are frequently emitted by *P. poliocephalus* during agonistic episodes suggesting that these calls may be a significant part of the threat display used by this species when fighting. It is possible that the ark calls of *P. poliocephalus* may be used to intimidate an opponent in an agonistic encounter by creating an illusion of greater size and fighting ability in the emitter than they actually possess. This is supported by the wing-flapping behaviour of *P. poliocephalus* that often occurs in association with the ark call. By flapping its wings an individual may be able to appear larger and more intimidating than they actually are.

Two tonal calls were recorded in *P. poliocephalus*; one emitted by adults, and one by juveniles. Adult *tonal* calls were predominantly emitted when an individual was escaping attack. The structure of this call is such that it is clearly transmitted to the primary receiver and will also alert conspecifics further away that a subordinate animal is approaching, possibly reducing the likelihood of their aggression towards that subordinate.

Adult *tonal* calls were made most frequently when an individual was crawling or flying away from an agonistic encounter, perhaps also reflecting a state of fear or anxiety in the emitter as it escaped. In *P. poliocephalus* it appears that *tonal* calls predominantly refer to the arousal state of the emitter and may also benefit conspecifics by providing them with information about a potential source of danger. The physical structures of the call are such that it is easy to locate and occurs at a higher frequency than any background noise that may be present, thus having the potential to be heard by all members of the colony.

The isolation call made by juvenile *P. poliocephalus* is high pitched, frequency modulated and contains a repeatable unit, which when emitted a number of times in succession increases the length of the call. The high fundamental frequency of this call in comparison to adult calls, may be partly due to the juveniles having a smaller body size and subsequently smaller sound producing structures. The juvenile isolation call of *P. poliocephalus* is exceedingly complex, and as such provides a considerable amount of information to the receiver, which is predominantly the juvenile's mother.

As a result of their smaller size, the call of the young occurs over a range of frequencies rarely reached by adult *P. poliocephalus* and as such is unlikely to be masked by adult calls or background noise within the colony. Also, the call is frequency modulated which means considerably more energy can be concentrated into the modulating frequency increasing both the signal-to-noise ratio and the intensity of the call. Further, the sharp beginning and end of each repeatable unit provides acoustic reference points which will arrive at each of the listener's two ears at two different times. By comparing the difference in arrival times at the two ears, the listener is able to more accurately locate the sources of the sound which in this instance is the juvenile calling from the night-time nursery.

Nelson (1964) placed the calls of *Pteropus* into two broad categories; (1) 'harsh' calls and (2) 'clear' calls. Based on the current study, three groups are perhaps more appropriate when describing the vocalisations of *P. poliocephalus*. It may be more comprehensive to apply the following classification; (1) the *harsh chuckles* and *ark* calls as 'harsh'; (2) the *tonal* calls as 'tonal'; and (3) the *tonal chuckles* and *chups* as 'intermediate' between the two. This may also be a more appropriate classification in terms of the behaviours associated with the three categories considering each one is emitted in a different context to the others.

Acknowledgements

We'd like to thank Martin Burd, Alan Lill, Martin Predavec and Craig Kingham for their knowledge and assistance, Ian Stewart for technical support and Gerry Quinn for statistical advice.

Literature Cited

Altringham, J. D., 1996. *Bats; biology and behaviour.* Oxford University Press.

Andrieu, A. J., 1963. Techniques used for the physical study of acoustic signals of animal origin. In *Acoustic behaviour of animals* ed by R. G. Busnel. Elsevier Publishing Company.

August, P. V., and Anderson, J. G. T., 1987. Mammal sounds and motivational- structural rules; a test of the hypothesis. *J. Mammal.* **68**: 1-9.

Biben, M., Symmes, D. and Bernhards D., 1989. Contour variables in vocal communication between squirrel monkey mothers and infants. *Dev. Psychobiol.* **22**: 617-631.

Brown, C. H., 1994. Sound Localization. In *Comparative hearing; mammals* ed by R. R. Fay and A. N. Popper. Springer-Verlag.

Brown, P. E., Brown, T. W. and Grinnell, A. D., 1983. Echolocation, development and vocal communication in the Lesser Bulldog bat, *Noctilio albiventris. Behav. Ecol. Sociobiol.* **13**: 279-298.

Busnel, R. G., 1963. On certain aspects of animal acoustic signals. In *Acoustic behaviour of animals* ed by R. G. Busnel. Elsevier Publishing Company.

de Fanis, E. and Jones, G., 1995. Post-natal growth, mother-infant interactions and development of vocalizations in the vespertilionid bat, *Plecotus auritus. J. Zool., Lond.* **235**: 85-97.

Fisler, G. F., 1970. Communication systems and organizational systems in three species of rodents. *Bull. S. Cal. Acad. Sci.* **69**: 43-51.

Grinnel, A. D., 1995. Hearing in bats: an overview. In Hearing by bats ed by A. N. Popper and R. R. Fay. Springer-Verlag.

Harcourt, A. H. and Stewart, K. J., 1996. Function and meaning of wild gorilla 'close' calls; correlations with rank and relatedness. *Behaviour.* **133**: 827-845.

Lewis, D. B. and Gower, D. M., 1980. *Biology of communication.* Blackie.

Linahan, N., 1995. The hearing and vocalisation of Australian marsupials. Unpublished honours thesis. Monash University.

Marler, P., 1967. Animal communication signals. *Science (Wash. D C).* **157**: 769-774.

Morton, E. S., 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *Am. Nat.* **111**: 855-869.

Morton, E. S., 1982. Grading, discreetness, redundancy and motivational-structural rules. In *Acoustic communication in birds; volume* I ed by D. E. Kroodsma, E. H. Miller and H. Ouellet. Academic Press Inc.

Nelson, J. E., 1964. Vocal communication in Australian Flying Foxes *(Pteropodidae; Megachiroptera). Z. Tierpsychol.* **21**: 857-870.

Nottebohm, F., 1972. The origins of vocal learning. *Am. Nat.* **106**: 116-140.

Ploog, D. and Melnechuk, T., 1967. Primate Communication. In *Neurosciences Research Progress Bulletin* ed by P. A. Diamond and C. M. LeBlanc. **7**: 423-506.

Pollack, G. D. and Casseday, J. H., 1989. *The neural basis of echolocation in bats*. Springer-Verlag.

Puddicombe, R., 1981. A behavioural study of the Grey-headed Flying-fox, *Pteropus poliocephalus*. Unpublished honours thesis. University of New England.

Scherer, K. R., 1985. Vocal affect signalling: a comparative approach. *Adv. Study Behav.* **15**: 189-244.

Schott, D., 1975. Quantitative analysis of the vocal repertoire of Squirrel Monkeys *(Saimiri sciureus). Z. Tierpsychol.* **38**: 225-250.

Suthers, R. A., 1988. The production of echolocation signals by bats and birds. In *Animal sonar; processes and performance* ed by P. E. Nachtigall and P. W. B. Moore. Plenum Press.

Symmes, D., Newman, J. D., Talmage-Riggs, G. and Lieblich, A. K., 1979. Individuality and stability of isolation peeps in Squirrel monkeys. *Anim. Behav.* **27**: 1142-1152.

Thorpe, W. H., 1967. Animal vocalization and communication. In *Brain mechanisms underlying speech and language* ed by C. H. Milikan. Green and Stratton.

Wickstrom, D. C., 1982. Factors to consider in recording avian sounds. In *Acoustic communication in birds; volume* I ed by D. E. Kroodsma, E. H. Miller and H. Ouellet. Academic Press Inc.

Zweifel, R. G., 1968. Effects of temperature, body size and hybridization on mating calls of toads, *Bufo a. americanus and Bufo woodhousii fowleri.* COPEIA. **1968**: 269-285.